UNIVERSITÉ DU QUÉBEC À MONTRÉAL

LA PERSISTANCE DES RONGEURS DÉSERTIQUES: IDENTIFIER LES IMPACTS DES REFUGES, DE LA DISPERSION ET DU PATRON DE PLUIE; VIA UNE SIMULATION SPATIO-TEMPORELLE

MÉMOIRE

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JULIEN CÉRÉ

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DÉDICACE

Deux personnes.

à Bill Vickery,
qui a été pour moi une source d'inspiration personnelle et professionnelle,
particulièrement en tant que modèle d'intégrité et de générosité dans le milieu
académique et scientifique.

à ma fille Émilie.
Puisses-tu reconnaître le beau dans le vrai.
Et l'inverse.

AVANT-PROPOS

Le projet initial de ma maîtrise en écologie comportementale sous la direction du professeur William Vickery portait sur la validation d'un modèle d'interactions interspécifiques autour d'une ressource non partageable. Notre objectif était de travailler avec trois espèces de sciuridés — le tamia rayé (Tamia striatus), et l'écureuil gris (Sciurus carolinensis) et roux (Tamiasciurus hudsonicus) — à l'arboretum Morgan à Saint-Anne-de-Bellevue.

Le modèle proposé suppose la rencontre d'un intrus et d'un individu exploitant une ressource non-partageable. Il aide à prédire, en premier lieu, le comportement optimal de l'arrivant, soit attaquer le découvreur, attendre et chaparder, ou encore rechercher d'autres ressources. En cas d'attaque, le découvreur peut défendre ou capituler et abandonner sa parcelle à l'intrus.

Pour valider le modèle, une série de mangeoires filmées étaient installées dans la forêt et le comportement des sciuridés était noté.

À l'été 2012, la campagne de terrain a servi d'étude préliminaire pour l'élaboration du protocole final. L'activité des sciuridés était modérée, quoiqu'inférieur à l'année précédente. La campagne de l'été 2013 était séparée en deux parties — préparation/ acclimatation et collecte des donnés finales. La présence des rongeurs était faible dans la première moitié de l'été et elle est devenue presque inexistante au moment de commencer la prise de donnée. De plus, des données d'intérêt nécessitaient la rencontre de deux individus, événement plus rare encore. Bien que l'activité des sciuridés ait un peu repris après un mois et demi de silence, les interactions étaient toujours aussi rares. Une collègue qui faisait son terrain au même endroit avec un protocole similaire utilisant aussi des caméras affirme n'avoir pas observé plus de cinq interactions dans les mangeoires pendant toute la campagne de terrain. Quoiqu'il

en soit, les données étaient largement insuffisantes pour observer des tendances. Une quelconque validation statistique était inconcevable.

Cette impossibilité de répondre à nos hypothèses nous a obligé à s'orienter vers un autre projet de recherche pour ma maîtrise.

J'aimerais tout de moins remercier l'arborétum Morgan et son directeur des opérations, John Watson, pour m'avoir permis d'échantillonner sur leur territoire. Je tiens aussi à remercier les membres de l'équipe qui m'ont aidé dans la capture et le marquage des individus, ainsi que pour les tâches de terrain — Stéphanie Tessier, Pascale Boulay, Mélinda Habel, Julie Pelletier, et Geneviève Collin.

La décision de changer de projet a été prise conjointement par mon directeur William Vickery et moi-même à des fins pédagogique. Ainsi, respectant mon intérêt grandissant pour la modélisation, j'ai entrepris le projet de compléter un modèle de simulation basé sur le désert Simpson. En 1997, en coopération avec le professeur Christopher Dickman de l'Université de Sydney, le professeur William Vickery a programmé une première version de ce modèle. La complexité du modèle et les limites technologiques ont empêché ce dernier d'analyser et d'interpréter les résultats de cette simulation. À l'été 2013, j'ai donc reprogrammé la simulation sous un autre langage plus rapide. Nous avons aussi travaillé à modifier quelques particularités du modèle, ainsi qu'à le simplifier en fixant plusieurs paramètres. Les simulations ont tournées sur 25 ordinateurs empruntés au Service de l'informatique et des télécommunication de l'Université de Québec à Montréal pendant une douzaine de fins de semaine.

Nous présentons donc les résultats de ce projet sous la forme de mémoire qui inclue un article scientifique (section en anglais) qui sera soumis ultérieurement à la revue *Ecological Modelling*.

TABLE DES MATIÈRES

LISTE DES FIGURES ET DES TABLEAUX

Tableau

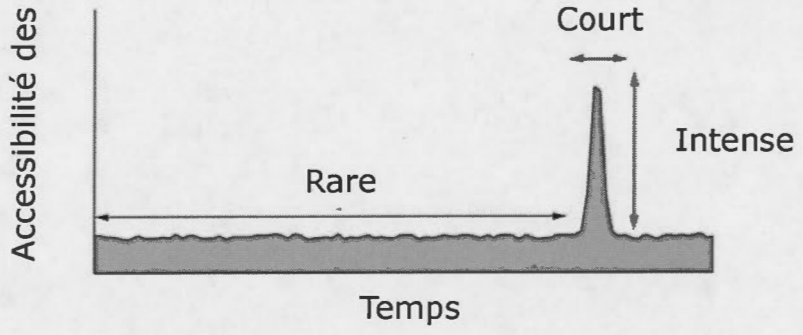
RÉSUMÉ

Dans le désert de Simpson en Australie, la dynamique des populations de petits rongeurs connaît d'importantes fluctuations dans le temps et dans l'espace. Certaines populations semblent disparaître pendant les périodes prolongées de sécheresse, mais ressurgissent en abondance après le retour des pluies, et donc des ressources. Nos hypothèses qui supporteraient la persistance de ces espèces reposent sur l'utilisation de refuges pendant la période sèche — survie d'une fraction de la population dans des parcelles moins arides — et sur la dispersion dans l'espace pour permettre l'exploitation de ressources autrement inaccessibles. Toutefois, les études empiriques n'ont pas l'échelle spatiale ni temporelle nécessaire pour tester ces hypothèses convenablement. Nous proposons donc un modèle de simulation qui explore les probabilités de persistance et la dynamique d'une population virtuelle de rongeurs dans une matrice cellulaire représentant un désert de 10,000 km^2 sur une période de 100 ans. Notre objectif est d'évaluer l'impact de ces facteurs — refuge et dispersion — sur la persistance d'une population selon des patrons de ressources plus ou moins abondantes et régulières. Après 295,648 simulations, il s'avère que la présence et la quantité de refuges, ainsi que la dispersion, deviennent essentiels pour la survie lorsque les précipitations sont modérément abondantes. Ces facteurs de persistance sont insuffisants quand les ressources sont très rares, et pas nécessaires lorsque les ressources sont abondantes. Une longue dispersal ou un grand nombre de refuges peuvent parfois compenser pour une faible valeur de l'autre facteur. Par opposition aux patrons de précipitations à faible variation inter-annuelle, un patron cyclique de précipitations qui simule l'influence de *La Niña* sur le continent Australien — une période prolongée de sécheresse suivi d'une période plus courte de précipitations plus abondantes — exacerbe significativement les probabilités de persistance. Dans de telles conditions, des refuges abondants et une dispersion sur de longue distance sont essentiels à la persistance d'une population de rongeurs dans le désert Simpson.

MOTS CLÉS: persistance, refuges, dispersion, précipitations, rongeurs, désert, simulation.

1. INTRODUCTION GÉNÉRALE

La dynamique des ressources dans un désert est souvent particulière. La quantité de ressources accessibles est souvent très faible. Cependant, des événements rares, intenses et courts — dits pulsations (voir figure 1.1) — inondent le milieu de



ressources (Yang *et al.*, 2008).

Figure 1.1: Les pulsations de ressources sont des événements rares, intenses, et courts d'augmentation de l'accessibilité des ressources. Tiré de Yang *et al.*, 2008.

Ces pulsations sont le résultat du patron de précipitations irrégulières. En effet, l'eau est un facteur limitant à la croissance dans les milieux désertiques. Donc, lorsqu'il pleut, les végétaux, suivis par les autrels groupes d'organismes, se développent rapidement. Ces précipitations sont souvent localisées sur une petite région dans un désert, souvent quelques kilomètres carrés (Sharon, 1972, 1981), alors les pulsations de ressources varient à la fois dans le temps et dans l'espace.

Dans le cas du désert Simpson en Australie, la variation inter-annuelle de fréquence de précipitations est grande, et elle est influencée par un facteur cyclique supplémentaire. Le phénomène *La Niña* est la contre-partie semi-indépendante d' *El*

Ce phénomène atmosphérique et océanographique a une influence importante sur les précipitations sur les continents (McGlone *et al.*, 1992).

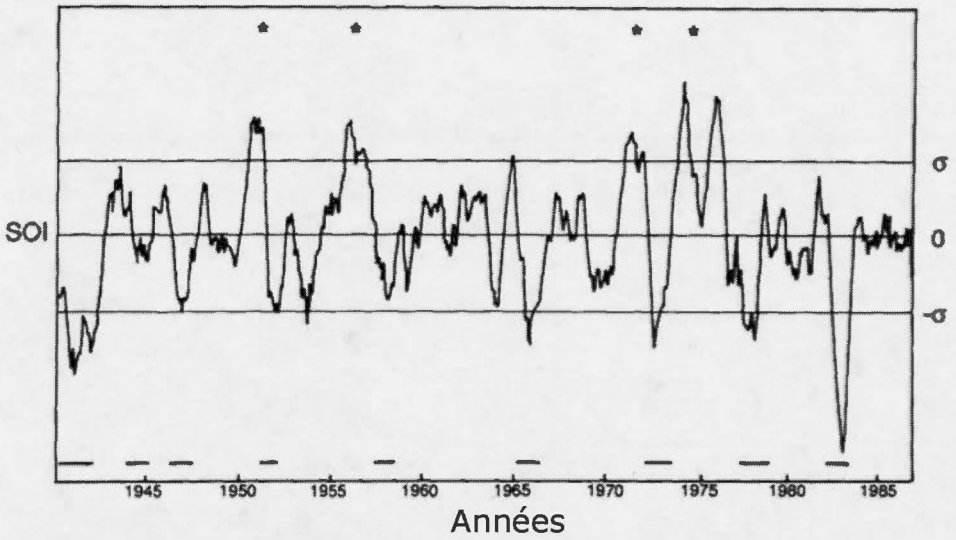


Figure 1.2: Les « Southern Oscillation Index » (ou SOI) entre 1940 et 1990. Les trois lignes horizontales représentent la moyenne à long terme et les écart-types supérieur et inférieur. Les lignes horizontales le long de l'axe des X indiquent le moment et la durée des périodes de sécheresse majeure dans l'Est de l'Australie. Tiré de Nicholls, 1991.

Cela ajoute une dynamique cyclique au patron de précipitations et de ressources dans le désert Simpson. Globalement, les périodes de grande sécheresse en Australie coïncident souvent avec un événement *El Niño* et les événements *La Niña* provoquent souvent une période humide, accompagné souvent par des pluies fortes et des inondations en Australie (voir figure 2.1) (Nicholls, 1991).

Comme les autres groupes, les populations de rongeurs — *Pseudomys hermannsburgensis, P. desertor, Notomys alexis, Mus domesticus* — connaissent de grandes fluctuations de densité dans le désert de Simpson (Dickman, C. R. *et al.*, 1999). Cette variation se voit premièrement sur l'échelle temporelle. Pendant les années de fortes pluies, les populations sont abondantes. Par contre, pendant les années de faibles précipitations, la densité de ces mêmes populations chute à des valeurs très faibles (voir figure 3.1). Pendant ces années, les observations de ces

espèces sur le terrain sont tellement rares qu'on peut croire ces espèces absentes ou même éteintes du paysage. Ces fluctuations sont aussi observables à l'échelle spatiale. Ces populations semblent parfois être présentes dans l'ensemble du territoire et d'autres fois contraintes à une région. Cela est le résultat des précipitations localisés.

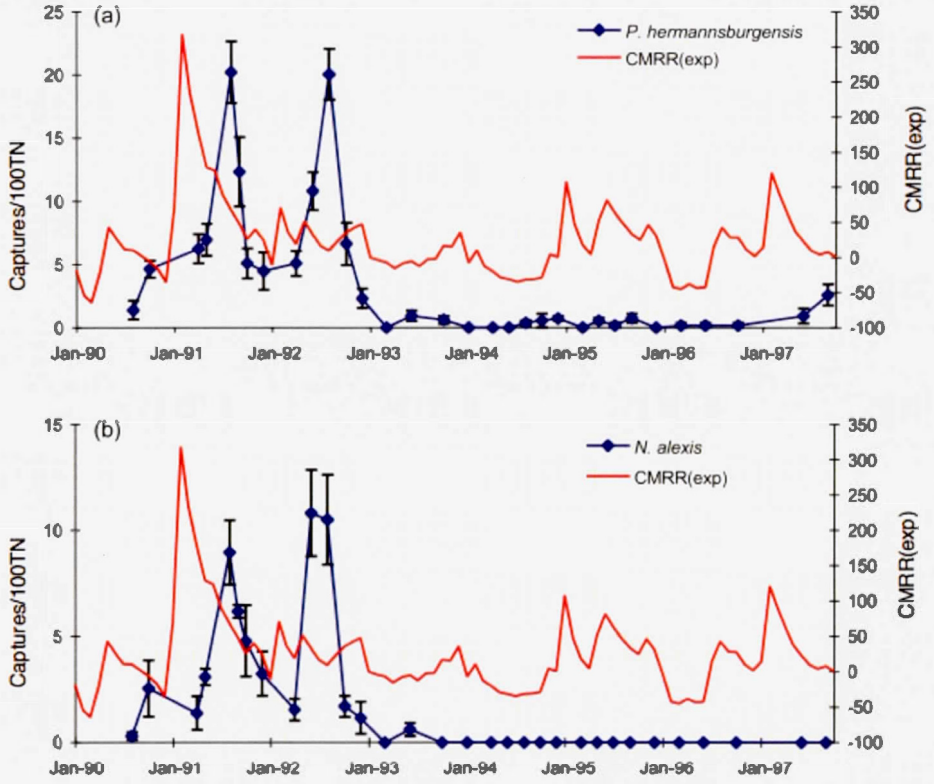


Figure 1.3: Captures pour 100 nuits-trappes (TN) pour Pseudomys hermannsburgensis (a) et Notomys alexis (b) de Aout 1990 à septembre 1997 au site du désert Simpson (moyenne ± s.e.). Aussi présenté est le cumulatif résiduel de précipitations mensuelles modifié par une fonction de décroissance exponentielle [. CMRR(exp)]. Tiré de Dickman *et al.*, 1999.

Nous nous interrogeons sur la période de faible densité de ces espèces et sur leur survie dans ces conditions. Nous voulons identifier les facteurs qui permettent la persistance de telles dynamiques.

Une des hypothèses qui a été amenée est l'utilisation de refuges. Un refuge est un endroit où les effets négatifs d'une perturbation sont moindres que dans le reste de l'environnement (Lancaster et Belyea, 1997). Les refuges supportent la résistance et résilience spatiale et temporelle face aux perturbations, comme les sécheresses (Magoulick et Kobza, 2003). Le principe de refuge s'applique à toutes les échelles spatiales et temporelles. En milieu aquatique par exemple, les canaux, bassins, plaines inondables, ainsi que les larges débris peuvent servir de refuges à différents groupes animales et végétales (Sedell et Reeves, 1990). Plusieurs espèces d'oiseaux aquatiques utilisent les « New England lagoons » comme refuges lors de périodes de sécheresses en Australie (White, 1987). Les micro-mammifères d' Eastern Cape, en Afrique du Sud, sont capturés en plus grandes abondance et diversité dans les bosquets d'arbustes pendant la saison sèche (Whittington-Jones *et al.*, 2008).

Dans le désert, un refuge peut être un oasis, un bosquet de végétation, ou encore une structure particulière du paysage. Pendant les années de sécheresse, une fraction de la population peut survivre dans ces endroits. Une fois les ressources plus abondantes dans le milieu, cette fraction de la population peut disperser et coloniser l'environnement riche.

Dans le désert Simpson, cette hypothèse a été testée sur trois espèces — *Pseudomys hermannsburgensis*, *Notomys alexis*, et *Dasycercus blythi*. On retrouve généralement ces espèces dans les prairies de spinifex, mais ils ne sont presque jamais capturées pendant les années de sécheresse (Dickman *et al.*, 2011). Dickman et collaborateurs (2011) ont émis l'hypothèse que les boisés ouverts d'*Acacia cambagei*, une espèce d'acacia endémique en Australie, pourraient servir de refuges à ces populations. Seulement *Pseudomys hermannsburgensis* a montré une préférence pour les boisés

pendant la période de sécheresse, mais n'y était pas contraint. Dickman et collaborateurs avancent qu'il n'est pas impossible que les autres espèces exploitent un autre type de refuge et que les techniques de capture seraient peu efficaces à estimer des populations en si faible densité (Dickman *et al.*, 2011). Beaucoup reste à faire au niveau de tester l'hypothèse de l'utilisation des refuges par les rongeurs désertiques.

L'utilisation des refuges n'est pas la seule stratégie possible de telles populations. Ces espèces évoluent dans un territoire irrégulier et fragmenté où les ressources sont rares et agglomérées. Cette dynamique peut être schématisée comme une matrice de parcelles occupées ou vacantes, plus ou moins riche en ressources, un peu à l'image d'une métapopulation (Hanski, 1991). À l'échelle locale, de rares précipitations provoquent une grande hétérogénéité de la capacité de support du milieu et des extinctions locales de populations sont possibles. Des parcelles riches mais vides devraient être colonisées par la dispersion des individus. Ce dernier principe, la dispersion, peut augmenter l'accessibilité d'un maximum de ressources pour les individus d'une population (Bowler et Benton, 2005). Une pluie qui touche une région où une espèce est absente génère des ressources inaccessibles pour cette espèce. Par contre, grâce à la dispersion individuelle, une espèce a l'occasion de s'installer dans les endroits plus riches. Il serait donc possible d'émettre l'hypothèse que la dispersion et la colonisation des parcelles riches en ressources pourrait être une stratégie pour survivre en période de sécheresse (Bowler et Benton, 2005). Par contre, les espèces ne dispersent pas toutes de la même façon. Des dispersion allant de moins d'un kilomètre à plus de dix kilomètres pour des périodes de deux mois ont été enregistrées pour certaines espèces de rongeurs du désert de Simpson (Dickman *et al.*, 1995).

En fait, les refuges et la dispersion doivent être intimement liés. Les individus retraités dans les refuges doivent pouvoir disperser au retour des pluies et des

ressources. Dans le cas contraire, les régions riches en ressources où la population est absente ne seront jamais recolonisées, et seulement les refuges seront occupés.

Notre objectif est donc de vérifier l'impact de ces facteurs de survie — l'utilisation de refuges et la dispersion — sur une population pendant une longue période de temps et sur une grande échelle spatiale. Nous aimerions tester dans quelle mesure ces facteurs peuvent améliorer les chances de survie et de persistance d'une espèce. Pour ce faire, nous proposons d'utiliser une simulation informatique pour programmer un désert virtuel spatialement explicite dans lequel on peut contrôler différents paramètres, similaire à un automate cellulaire (Wiegand *et al.*, 1999). Une matrice de 100 cellules par 100 cellules représentera un désert de 10 000 km^2, et une boucle de 100 pas de temps simule une période de cent ans.

Notre population fictive évoluera alors sur une longue échelle temporelle selon l'abondance et la distribution spatiale des ressources. En effet, en manipulant les différents paramètres, nous pouvons expérimenter sur notre population virtuelle plusieurs combinaisons de fréquences et de patrons de précipitations. Instinctivement, une quantité croissante et régulière de précipitations devrait aussi influencer positivement les probabilités de persistance.

Les probabilités de persistance seront donc estimées selon la quantité de refuges et la distance maximale de dispersion.

Nous émettons donc les hypothèses que les probabilités de persistance augmenteront avec le nombre de refuges dans l'espace et avec la distance de dispersion. Nous ferons aussi varier les ressources — fréquence annuelle et patrons de précipitations — pour tester les limites des facteurs de persistance selon l'environnement.

2. ARTICLE

Unlikely survival of rodents in the desert: exploring the impacts of refugia, dispersal, and rainfall through a spatio-temporal simulation approach

JULIEN CÉRÉ, WILLIAM L. VICKERY and Christopher R. Dickman

Département des sciences biologiques, Université du Québec à Montréal and Desert Ecology Research Group, School of Biological Sciences, University of Sydney

Article to be submitted

2.1 Abstract

In arid environments, animal population dynamics commonly follow resource pulses in time and space that are driven by irregular and local rainfall events. During drought, the population densities of many species fall so low as to be undetectable, posing questions about how they persist and minimize the chance of extinction. When rainfall and resources return, populations recover and again become abundant and occur over large areas. Taking desert rodents as model organisms, we hypothesized firstly that a fraction of the population may survive in refugia — less arid patches in the landscape — and colonize the broader environment again after drought-breaking rains. Secondly, we predicted that dispersal should enhance the accessibility of patchy resources. We use a spatio-temporal simulation approach to test these hypotheses on a large temporal and spatial scale. We programmed a virtual desert (100 × 100 matrix) in which a virtual population changes over the course of 100 time steps representing 100 years. When rainfall events were scarce, refugia and dispersal were insufficient to maintain persistence, and when they were abundant, these factors were not necessary. At moderate rainfall frequencies, refugia and dispersal were essential for population persistence, and long-distance dispersers needed fewer refugia than their short-distance counterparts. With cyclic rainfall patterns mimicking the influence of the *El Niño-Southern Oscillation*, that is, long droughts punctuated by short wet periods, rodents were predicted to persist only with abundant refugia and long distance dispersal.

Keywords: persistence, refugia, dispersal, rainfalls, rodent population, desert, simulation

2.2 Introduction

In most desert environments, rainfall is a limiting factor that causes a resource-pulse dynamic in both primary producers and consumers. Yang *et al.* (2008) defined resource pulses as rare, brief and intense resource inputs in time and space. Rainfall events may be widespread, but in arid environments are often more local and prescribed (Sharon, 1972, 1981) so the resources they generate tend to be scattered and patchy (Günster, 1995). Resource-limited populations usually exhibit spatial and temporal dynamics that reflect the availability of their limiting resources (Brown *et al.*, 1972; Letnic et Dickman, 2005; Rosenzweig et Winakur, 1969); thus in arid environments, in particular, populations can fluctuate greatly in time and space (Brown et Zeng, 1989; Whitford, 1976). In desert mammals, for example, it is not uncommon to see populations persisting at very low density, close to extinction, over periods of many years (Brown et Heske, 1990; Pavey et Nano, 2013). Interestingly, we also see booms in the density of these same species, usually after major rainfall events (Letnic et Dickman, 2005, 2010; Plomley, 1972). How can such species avoid extinction and persist in time and space when their densities are so low during drought periods?

Some desert organisms ride out periods of scant resources by estivating or entering desiccation-resistant life stages, but such strategies are less available to vertebrates and especially to homeotherms (Geiser et Pavey, 2007). In many hostile environments, instead, such species retreat into refugia when conditions are poor (Chester et Robson, 2011; Milstead *et al.*, 2007). According to Lancaster and Brelyea (1997), a refugium is a place or time where the negative effects of a disturbance are lower than in the surrounding area. Milstead *et al.* (2007) compared the spatial

distribution of desert rodents in different habitats during dry and wet periods, and found that populations persisted in some habitats long term, but were otherwise absent elsewhere during dry periods. Perturbations such as drought may lead to increased spacing between refugium habitats, and therefore mobility of organisms should also play a large role in population persistence (Magoulick et Kobza, 2003). When conditions improve, individuals surviving in refugia can disperse and colonize surrounding areas. Dispersal and colonization therefore may be crucial for maintaining populations across desert landscapes.

This spatio-temporal dynamic resembles the behavior of a metapopulation exploiting a patchy environment, where resource scarcity and aggregation are typical (Hanski, 1991). In contrast to Levins' metapopulation concept and subsequent models (Hanski, 1991), however, hospitable patches in the desert are likely to be variable in space and time, and in quantity and quality. Nonetheless, dispersal will still be vital if animals are to reach and populate unoccupied patches (Bowler et Benton, 2005); dispersal and colonization should help a low density population to exploit scarce and otherwise unavailable resources (Sepulveda et Marczak, 2011). If dispersal and colonization suffice to ensure population persistence or even expansion, specific refugia will not be required.

In addition to spatio-temporal variation in local rainfall, arid regions are subject also to marked inter-annual fluctuations in precipitation frequency and intensity due to the cyclic *El Niño – La Niña* phenomenon (Holmgren *et al.*, 2001). Most commonly referred to as the *El Niño* – Southern Oscillation (ENSO) owing to the predominance of its effects in the southern hemisphere, this oceanic oscillation leads, amongst other things, to strong perturbations in rainfall patterns on land (Nicholls, 1991, Allan et al. 1996). The *La Niña* component of the oscillation coincides with intense wet periods

often accompanied by flooding in Australia and with drought conditions in western South America, with *El Niño* having the reverse effects on both continents (Nicholls, 1991). The prevailing ENSO pattern of consecutive drought years punctuated by less frequent wet years can be expected to be a key driver of resource dynamics (Greenville et al. 2012), and should therefore be taken into account when explaining the persistence of desert organisms.

In this paper, we use the Simpson Desert in central Australia as a case study example to explore the effects of different rainfall regimes, refugia and dispersal ability on a model group of organisms—rodents. The Simpson Desert supports at least six species of rodents, all of which show dramatic fluctuations in their populations (Dickman, *et al.*, 1999; Letnic et Dickman, 2005). The long-haired rat (*Rattus villosissimus*), for example, may be absent from trapping records for up to 20 years, appear in large numbers after heavy rains and then retreat again to widely spaced refugia along drainage lines (Greenville et al. 2013). By contrast, the sandy inland mouse (*Pseudomys hermannsburgensis*) persists at low very numbers (<1 animal per hectare) during droughts and increases 40-60 fold after rain; it uses small (< 10 ha) patches of woodland embedded in the broader sand dune environment as drought-refugia (Dickman *et al.* 2011). Other species, such as the spinifex hopping-mouse (*Notomys alexis*), may also benefit from the woodland during dry periods, but appear to use even smaller and widely dispersed refugia (Dickman *et al.* 2011). There is uneven capacity for dispersal among these species (< 1 km to > 10 km), with the longest movements towards areas that have recently received local rainfall (Dickman, *et al.*, 1995).

Field studies of desert rodent populations are most often carried out for periods of several years (e.g. Free *et al.*, 2013), with few lasting longer than two decades

(Dickman, *et al.*, 2011; Brown et Heske, 1990; Whitford, 1976) or achieving broad spatial coverage. Although empirical data from such studies are exhaustive, they are unable to present a holistic scheme that can explain the persistence of rodents in arid environments long term (Dickman, *et al.*, 1999). Here, we are interested in a long term and geographically widespread scale, and so have approached the problem of population persistence via a spatially and temporally explicit simulation model. Thus, we merge a spatially explicit cellular automaton model (Kari, 2005) with demographic components. This permits us to explore the possible parameters that drive the spatial dynamics of rodent populations over long periods, up to 100 years.

Using Simpson Desert data to help inform our model structure, we explore the influences of rainfall, drought refugia and dispersal ability on the population persistence of desert rodents. We test three hypotheses: 1) an increasing number of drought refugia will enhance the chance of population persistence during drought periods, 2) increasing dispersal distance will improve animals' access to resources and hence increase population density and persistence probability, and 3) increasing rain frequency and regularity will enhance both the persistence probability and population density of rodent populations.

2.3 The model

We used a spatio-temporal simulation similar to a cellular automaton (Wolfram, 1984) to test our hypotheses about the dynamics of desert rodent populations. A cellular automaton consists of an array of cells that interact with their neighbors (Green, 1989). In our case, the array represents a desert landscape where each cell represents an equal portion of the desert.

We programmed a series of simulations of a 10 000 km² desert (100 × 100 matrix) over 100 years. Using *R* software (Gentleman et Ihaka, 1997), the simulations were programmed as a pile of matrices where each cell was connected with its equivalents on the other matrices (see Annex A for the script). The method was both simple and quick to run. The principal matrices were: refugia (*O*), rainfall (*R*), support capacity (*K*), and population (*N*).

The factors marked below with * are parameters, and the numbers in parenthesis () are the chosen fixed values. Each simulation began with the random positioning of a predetermined number of refugium cells* (matrix *O*). Support capacity limits were then set for desert and refugium cells (matrix *K*). For the sake of simplicity, the programmed refugia were immune to total depletion (minimal support capacity, 100), and to extinction (minimal population, 20). The initial population*(2) was also set in the population matrix (*N*). The loop, a series of events repeated 100 times, is summarized in Table 1. Firstly, precipitations were distributed randomly in the 10 000 km² region of the desert, and their frequency was subject to a predetermined mean of annual rainfalls and a specific rainfall pattern (explained below, matrix *R*). Each cell had the same probability of being affected by a rainfall. A rainfall event affected nine

cells* (9 km²) and boosted the support capacity* of those cells (adding 1000/rainfall to *K* in matrix *K*). As mentioned above, the choice of such a small area was based on empirical observations and published desert rainfall dynamics (Sharon, 1972, 1981). In this way, each cell had its own support capacity which varied through time, increasing when it rained and decreasing* (during the depletion events) when it did not. Secondly, the population in each cell grew* (r = 5) according to the logistic model (Verhulst, 1845)(matrix *N*, depending on matrix *K*). The growth rate was high because our time lapse was years and rodents usually reproduce more than once per year and may, in some species such as the long-haired rat, have up to ten offspring per litter (Taylor and Horner 1973, Watts and Aslin 1981). Thirdly, to simulate dispersal as described above, we extracted the portion of the population (*N*) above the support capacity plus ten percent from each cell. These individuals then dispersed to the four neighboring cells. We called that a 'dispersal event'. An individual could then disperse one kilometer (one cell) or further if we allowed multiple dispersal events per year*. The number of dispersal events determined the maximum dispersal distance. The actual dispersal distance of an individual is due largely to resource distribution because individuals stayed in a cell if the population had not reached support capacity. However, when neighboring cells were arid (low support capacity), individuals could go as far as the maximum dispersal distance. As ability to disperse can be an individual trait, with variation within a population, our dispersal approach was chosen to represent a mean of that variation. At the end of the dispersal events, the portion of the population that still exceeded the support capacity was eliminated. In our model, when a population in a cell reached zero, it went to local extinction, and only a migrant could repopulate that cell. A population over 0 but less than 1 also had a chance to go extinct. The probability that a fraction of individuals would survive in a cell was equal to its fractional value (between zero and 1).

The last event in our loop was resource depletion due to resource exploitation, leaching and evaporation. The support capacity (each cell of the entire matrix K) was reduced by a depletion factor* (0.65). The resulting support capacity was taken into account during the next year's reproduction period. This series of events was repeated 100 times to simulate a period of one hundred years.

Table 2.1: Summary steps of the simulation

	Events	Details	Matrix
0	Refugia	Predetermined number randomly installed on the matrix	O
		100 times loop	
1	Rainfalls	9 km^2 : Random in space and number (according to a predetermined mean and rainfall pattern)	R
2	Change in support capacity	+ 1000 K to support capacity of cells touched by rainfall	K
3	Growth of the population	Logistic growth	N
4	Dispersal	The population exceeding the support capacity + 10% disperse to the 4 neighboring cells (1/4 in each)	N
5	Mortality & Local extinction	Elimination of excess population & probability of extinction for fraction of individual.	N
6	Resource depletion	Drying up of the resource, i.e. support capacity is reduced by 65 %	K

In order to test our hypotheses, we explored the following parameters: number of refugia (0, 1, 10, 50, 100, 200, 350), and the number of dispersal events (maximum dispersal distance; 1, 2, 3, 4, 5, 8 kilometers). Resource availability being the main

limiting factor, we also varied the quantity and frequency of rainfalls to examine possible interactions between parameters.

Based on a 108 year database, the Simpson desert has received a mean of 22,6 days of rain per year, with only 5,7 of them being rain of more than 10 mm (Australian Bureau of Meteorology, 2014). Treatments included several mean numbers of rainfalls per year (5, 12, 25, 37, 50) organized by four different patterns of regular or irregular rainfalls. As shown in Fig. 1, the first pattern represented a fixed number of rainfalls per year (i.e. the mean), and the second a random uniform distribution around the mean with the lowest limits being 1. The other two patterns mimicked fluctuations due to ENSO, with a nine year cycle: seven years of low frequency rainfalls and two years of high frequency rainfalls. The ENSO phenomenon and its implications for continental precipitation are still variable, so we used two patterns: a proportional one and an arid one. The main difference lies in the gap between the drought and wet periods. For the proportional pattern, there was large inter-annual variation and a moderate difference in precipitation range between drought and wet periods. For the arid pattern, the drought year events were always between 1 and 6 rainfalls; we varied wet year precipitation, with a fixed, low inter-annual variation. Some other variables* described above (growth rate, rainfall area) were fixed based on observations from the Simpson Desert. Others have been quantified previously and their influence has been characterized as minimal (initial support capacity, initial population) or highly predictable (resource depletion factor, resources generated by rainfall). We aimed to generate arid conditions to examine the different dynamics and interactions of the parameters of interest — number of refugia, and maximum distance of dispersal — under extinction pressure (influenced by the mean annual rainfall frequency, and the rainfall pattern).

For our analyses, we observed the binomial outcome of each simulation: extinction (0) was declared when the population outside the refugia reached zero, and otherwise persistence (1). In cases of persistence, we extracted the total population, abundance and density of occupied cells ($\geq$1 individuals) for each year of the last 25 years. The first 75 years were considered to be the adaptation period of the population to the parameter. We arbitrarily chose the last 25 years of the simulation to represent the response of the population in terms of permanent dynamics. In our analysis, we excluded the refugium cells. We also calculated the coefficient of variation for all the demographic parameters listed above.

We performed 295,648 simulations to test our hypotheses. For statistical analysis using *R* software (R Development Core Team, 2008), we constructed a generalized linear model for the persistence probability (with a binomial distribution: 0 for extinction of the population and 1 for persistence), and fit least-squares for the demographic parameters: spatial distribution (mean number of occupied cells) and mean density (mean number of individuals in occupied cells). Our independent variables were the mean number of annual rainfalls, the number of refugia, the number of dispersal events, and the interaction of the latter two.

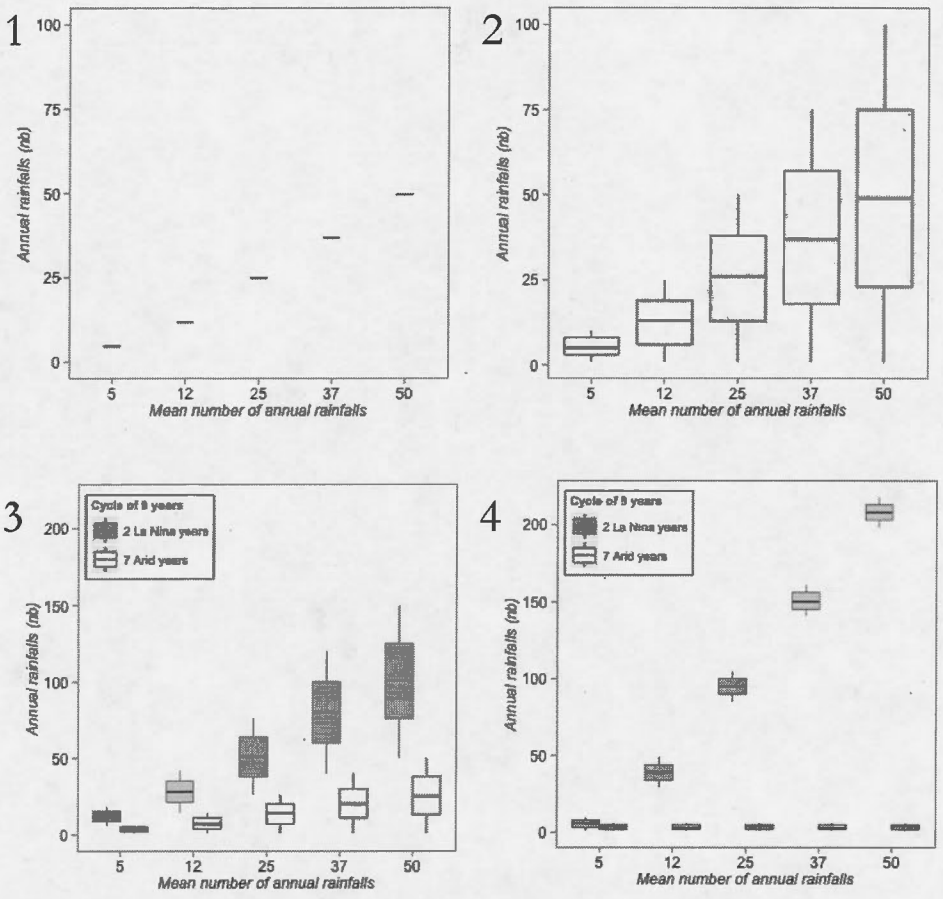


Figure 2.1: Range in the number of annual rainfalls under the four contrasting patterns: 1. Constant rainfalls, 2. Variable with a uniform distribution, 3. ENSO cyclic dynamic (proportional), 4. ENSO cyclic dynamic (arid)

2.4 Results

We will not emphasize actual numbers in our analysis of the results. The reason is that the results are associated with a series of fixed parameters. If we modify one, we may end up with slightly different results. The thresholds might shift, but the relationship will stay, and that is what we want to point out. Details of the statistical analysis are shown in Table 2.

2.4.1 Population Persistence rates

2.4.1.1 Rainfall

The annual mean rainfall frequency significantly improved the probability of population persistence ($p<0.001$, mean odds ratio = 1.136).

The fixed and the random rainfall patterns showed very similar results (see Fig. 2.2, glm, $p = 0.308$). When rains were abundant (more than 25 rainfall events per year), persistence was almost guaranteed unless animals dispersed poorly. This is an important threshold because persistence without actual refugia becomes possible. For these patterns, at low annual rainfall frequency (less than 25), persistence depended on the number of refugia and the distance of dispersal.

ENSO proportional ($p<0.001$, odds ratio = 0,019) and arid ($p<0.001$, odds ratio = 0,0008) patterns yielded lower persistence rates than the fixed and random patterns (p

= 0.308, odds ratio = 1/1.023). The arid pattern produced lower persistence than the proportional pattern. Both produced the same logistic relation of persistence, shifted to the right of the curves produced by the fixed and random patterns (Fig. 2.3). This means that extinction happened for a wider range of values of all the parameters and, unlike non-cyclic patterns, persistence cannot be assured without refugia or dispersal.

With the cyclic rainfall patterns, there was a more gradual rise in the persistence rate as a function of rainfall frequency compared to the non-cyclic patterns. Annual mean rainfall had less influence on the probability of population persistence under the arid pattern than under the other patterns (odds ratio; arid = 1.017, proportional = 1.132, fixed/random = 1.198). With the arid pattern, maximum persistence was only attained with a high number of refugia and long-range dispersal.

2.4.1.2 Refugia

The number of refugia also significantly improved the probability of population persistence in our simulation ($p<0.001$, mean odds ratio = 1.018). When rainfall was scarce, extinction was inevitable even with an intermediate abundance of refugia (Fig. 2.2, top-left corner). A minimum number of refugia was necessary to improve persistence rate and, over that threshold (usually between 10 and 50 refugia), adding more refugia did not change the persistence rate much and a short distance of dispersal was enough to assure persistence (top-right corner). That threshold is higher for the cyclic patterns (Fig. 2.3) and depended on rainfall abundance and pattern. In these cases, abundant refugia were essential for persistence.

Otherwise, if rainfalls are frequent and regular (non-cyclic pattern), only very few refugia or very short dispersal distances are enough to raise the already high probability of persistence to the maximum (bottom of Fig. 2.2).

2.4.1.3 Dispersal

The distance of dispersal strongly improved the probability of population persistence in our simulations ($p<0.001$, mean odds ratio = 2.204). Dispersal seemed to have a large influence in comparison to the other parameters. However, we should note that dispersal was measured on a different scale from other parameters. For the fixed and random patterns, a short distance was usually enough to assure persistence. Unlike the refugium relationship with persistence, the first kilometers of dispersion are the most important. At low rainfall frequency, it takes many refugia and wide dispersal to get a moderate chance of persistence, especially under the arid pattern. Adding more refugia slowly lessens the distance required to attain the maximal persistence rate. On the other hand, farther dispersal can make the refugia unnecessary.

Under the ENSO pattern, dispersal, especially long distance, was necessary for persistence. Cyclic patterns had higher odds ratios for dispersal (fixed/random = 1.760, proportional = 2.147, arid = 2.707). Therefore, migrating in cyclic rainfall patterns was more profitable than in the other patterns (arid > proportional > fixed/ random). In the four patterns, when rainfall frequency was low and refugia were few, no dispersal was sufficient to insure persistence (Fig. 2.2, top-left corner).

The interaction between dispersal and refugia was positive and significant ($p<0.001$), so these parameters had a synergistic effect. The contribution to the probability of population persistence from the two is greater than the sum of their individual influences.

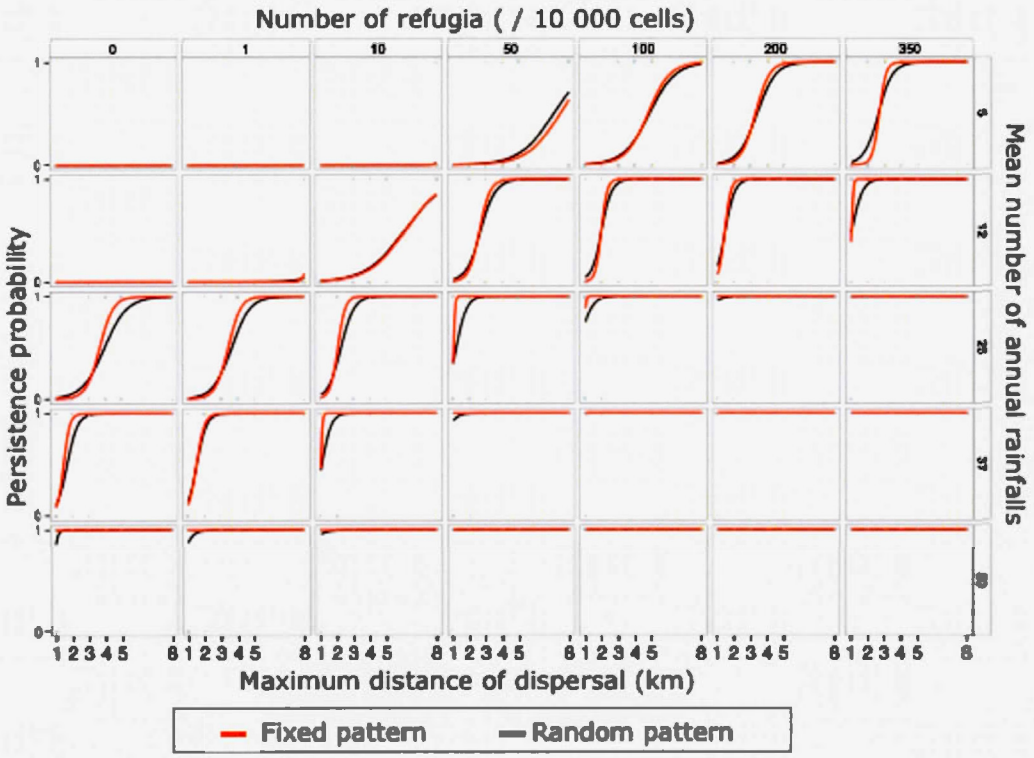


Figure 2.2: Trellis displays of the persistence rate for model populations of desert rodents with regard to the distance of dispersal, numbers of refugia (top axis) and fixed and random patterns in the annual mean number of rainfalls (right-hand axis)

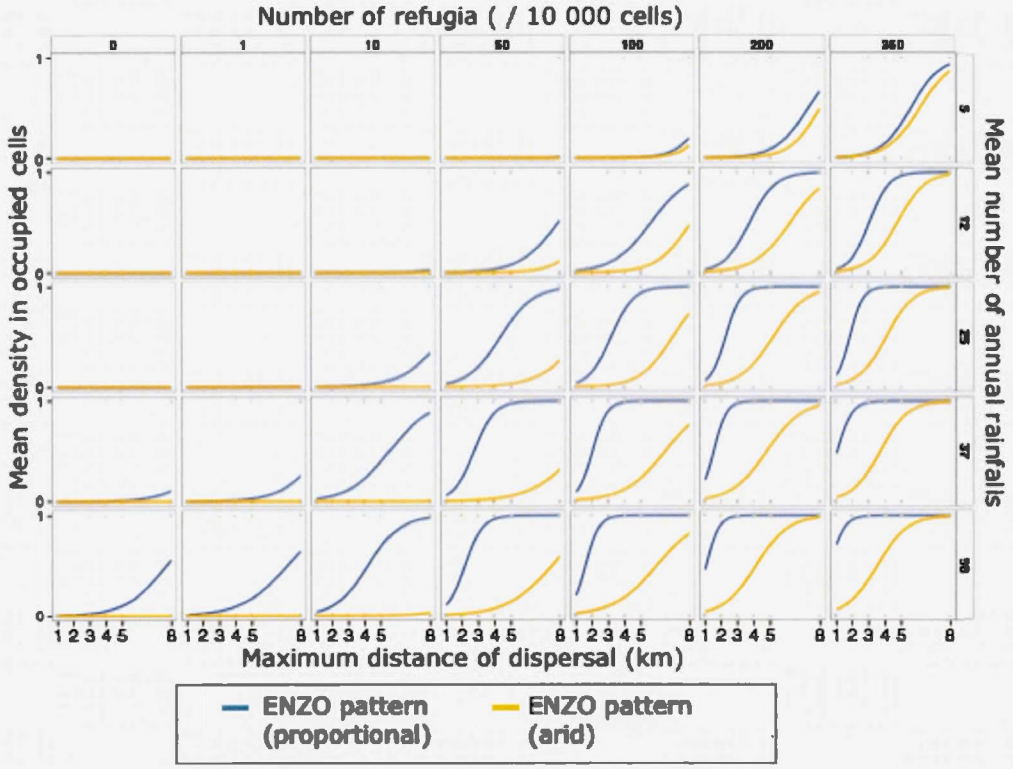


Figure 2.3: Trellis displays of the persistence rate for model populations of desert rodents with regard to the distance of dispersal, numbers of refugia (top axis) and different ENSO patterns for the annual mean number of rainfalls (right-hand axis)

Table 2.2: Generalized linear models (binomial) of the persistence rate of model populations of desert rodents as a function of distance of dispersal, the number of refugia, and mean number of annual rainfalls for each rainfall pattern. The table includes the odds ratio (the increase in the persistence rate for a unit increase in the independent variable) and its 95% confidence interval and the probability that the independent variable has a significant effect on persistence rate.

Fixed and random patterns are shown together because they show no significant difference

Parameters	Odds Ratio	2,5 %	97,5 %	$p(>\|z\|)$
Fixed & Random pattern (odds ratio= 1 & 1.023 , p=0.308)				
Intercept	**0,0003**	0,0003	0,0005	**< 0,001**
Maximal distance of dispersal	**1,7602**	1,6853	1,8390	**< 0,001**
Number of refugia	**1,0213**	1,0205	1,0220	**< 0,001**
Mean number of annual rainfalls	**1,1984**	1,1877	1,2094	**< 0,001**
Dispersal*Refugia	**1,0294**	1,0264	1,0325	**< 0,001**
Proportional cyclic pattern (odds ratio= 0.019 , $p < 0.001$)				
Intercept	**0,0001**	0,0001	0,0001	**< 0,001**
Maximal distance of dispersal	**2,1473**	2,0947	2,2017	**< 0,001**
Number of refugia	**1,0169**	1,0166	1,0172	**< 0,001**
Mean number of annual rainfalls	**1,1324**	1,1281	1,1367	**< 0,001**
Dispersal*Refugia	**0,9967**	0,9960	0,9973	**< 0,001**
Arid cyclic pattern (odds ratio= 0.0008 , $p < 0.001$)				
Intercept	**0,00001**	0,00001	0,00002	**< 0,001**
Maximal distance of dispersal	**2,70669**	2,58550	2,83559	**< 0,001**
Number of refugia	**1,01655**	1,01610	1,01700	**< 0,001**
Mean number of annual rainfalls	**1,07866**	1,07110	1,08635	**< 0,001**
Dispersal*Refugia	**0,99619**	0,99506	0,99733	**< 0,001**

2.4.2 POPULATION DYNAMICS

2.4.2.1 Spatial distribution

Adding refugia (fit-least square, estimate = 1.506, $p<0.001$), migrating longer distances (fit-least square, estimate = 86.312, $p<0.001$), and adding rainfalls (fit-least square, estimate = 20.678, $p<0.001$) increased significantly the number of cells occupied in the simulations. The maximum spatial occupation of a population in our simulations did not exceed 3000 cells, less than a third of the model desert (Fig. 2.4). At low rainfall frequency, the number of occupied cells behaved very similarly between the four rainfall patterns. The gap is more important at higher frequencies where the non-cyclic patterns (fixed and random) allow species to occupy significantly more space. For the two cyclic patterns, the spatial distribution was very similar but stayed low, rarely covering more than a tenth of the desert.

Longer dispersal distances greatly increased the number of occupied cells, up to a plateau beyond which dispersal had no further effect on cell occupancy. Although their effect was significant, refuges had very low influence on spatial occupancy (estimate = 1.507).

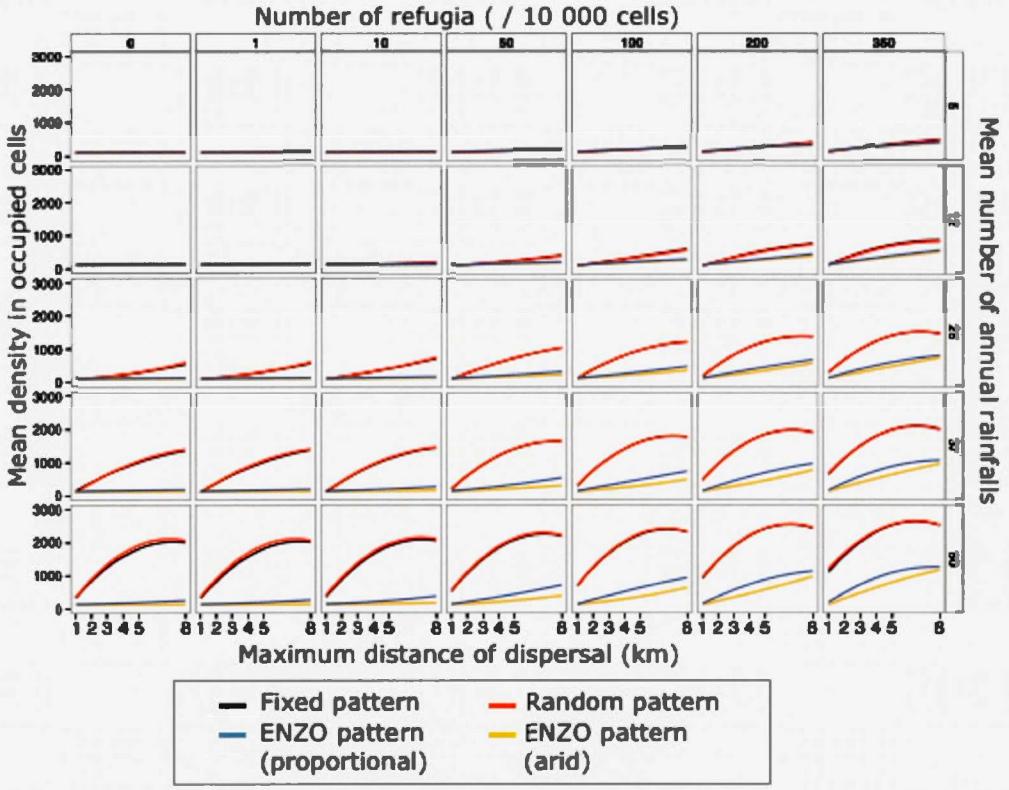


Figure 2.4: Trellis displays of the mean number of occupied cells (> 1 ind.) for model populations of desert rodents with regard to the distance of dispersal, numbers of refugia (top axis) and different patterns for the annual mean number of rainfalls (right-hand axis)

Table 2.3: Fit least-square models of the mean number of occupied cells (> 1 ind.) of model populations of desert rodents as a function of distance of dispersal, the number of refugia, and mean number of annual rainfalls. (R^2 adjusted = 0.2112)

Parameters	Estimate	Std. Error	T value	$p(>\|z\|)$
Intercept	-480,416	2,023	-237,530	**< 0,001**
Maximal distance of dispersal	86,312	0,337	255,790	**< 0,001**
Number of refugia	1,506	0,006	243,140	**< 0,001**
Mean number of annual rainfalls	20,678	0,047	442,810	**< 0,001**
Dispersal*Refugia	0,207	0,003	76,270	**< 0,001**

2.4.2.2 Density

Overall, rainfall frequency (fit-least square, estimate = 0.447, $p<0.001$), number of refugia (fit-least square, estimate = 0.050, $p<0.001$), and the distance of dispersal (fit-least square, estimate = 0.894, $p<0.001$) had a significant but small influence on the mean density in occupied cells (Fig. 2.5). The density does not exceed 50 individuals in occupied cells (1 km^2).

For the cyclic rainfall patterns, densities were lower than fixed and random patterns at high rainfall frequency, but the difference was not as great as it was for the number of cells occupied or for the probability of species persistence.

Spatial occupation and density data show the same pattern as persistence: when rainfall and refugia become more scarce and animals migrate shorter distances, density gets lower, fewer cells are occupied and finally populations go extinct.

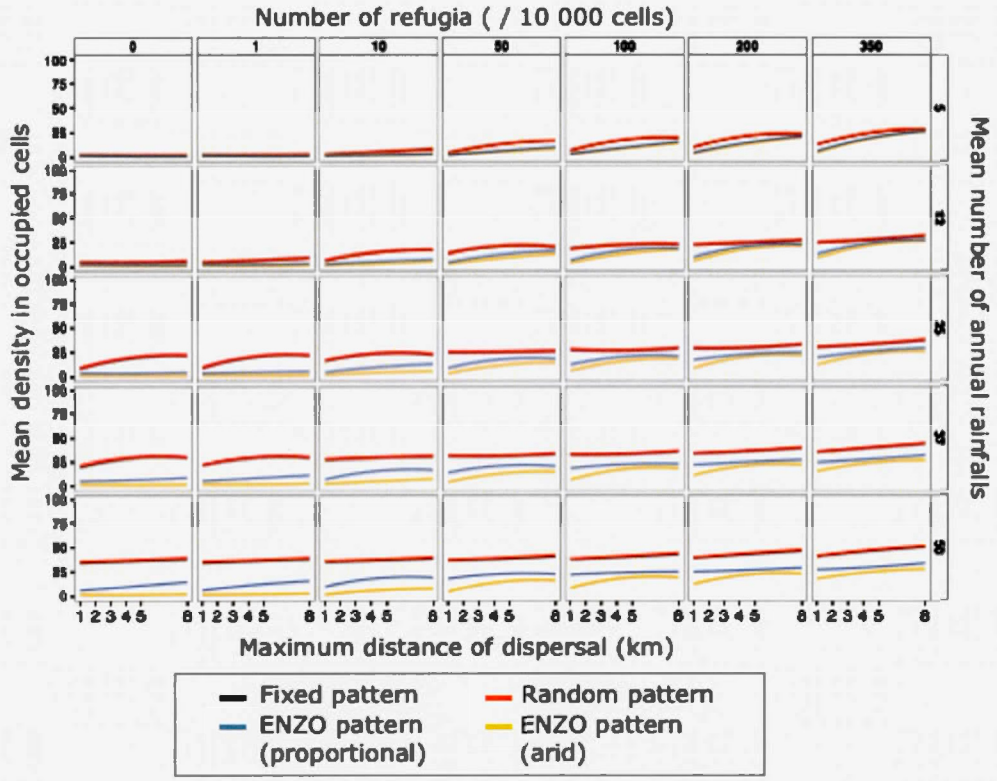


Figure 2.5: Trellis displays of the density of occupied cells (> 1 ind.) for model populations of desert rodents with regard to the distance of dispersal, numbers of refugia (top axis) and different patterns for the annual mean number of rainfalls (right-hand axis)

Table 2.4: Fit least-square models of the density of occupied cells (> 1 ind.) of model populations of desert rodents as a function of distance of dispersal, the number of refugia, and mean number of annual rainfalls. (R^2 adjusted = 0.5553)

Parameters	Estimate	Std. Error	T value	$p(>\|z\|)$
Intercept	-0,734	0,043	-17,160	**< 0,001**
Maximal distance of dispersal	0,894	0,007	125,330	**< 0,001**
Number of refugia	0,050	0,000	379,400	**< 0,001**
Mean number of annual rainfalls	0,447	0,001	452,450	**< 0,001**
Dispersal*Refugia	0,003	0,000	47,310	**< 0,001**

2.5 Discussion

As predicted, the two persistence factors — refugia and dispersion — enhance persistence probability (hypothesis 1 and 2). When rainfalls were rare, a critical minimum of refugia was needed before that factor could ensure at least some persistence probability. The influence of dispersal was more direct. The first few kilometers of dispersion were the most important by increasing the probability of persistence from near zero to almost 100%. Empirically, Dickman, *et al.* (1995) observed that dispersal distances are usually shorter than our maximal treatment of eight km for most Simpson desert small mammals. It is thus likely that our model covers the relevant range of this parameter. Further, there were interactions between factors. In fact, the effects of refugia and dispersal were essential, compensatory and synergistic. When rainfall frequency was scarce and/or cyclic, refugia and dispersal were necessary for persistence. This was in contrast to when precipitation was regular and plentiful; very few, if any refugia or dispersal were needed. The compensatory interaction comes from the fact that a high value of one strategy may compensate for a low value of the other strategy. A large scale disperser needs fewer refugia to survive than a more sedentary species. In the same vein, in a refugia-abundant environment, a species would not need to migrate as far, thus saving on the cost of dispersal. In the end, due to synergy, betting on both strategies is the most profitable solution. The influence of both refugia and dispersal was greater than the sum of the two effects taken individually. Although not included in our model, dispersion cost could limit the distance to which an animal is willing to disperse. In our model, it would have lowered the impact of dispersal on the persistence probability.

In the simulation, the whole desert acted as a temporally and spatially dynamic source-sink matrix for the global population. The refugia were then a permanent source while many parts of the desert where lack of resources depleted population density were sinks. A refugium-source is useless until the surrounding environment is welcoming. When isolated, a refugium will send dispersal individuals to their death. The dispersal from a refugium is efficient only when precipitation falls in the surrounding area. The probability of that happening regularly determines the efficiency of refugia. It is similar for dispersal distance. Effectively, Dickman *et al.* (2010) showed that rodents in Simpson desert were more mobile during their burst phase as a population. Knowing that there is a cost to dispersal, the odds of meeting a welcoming area (recently touched by rainfalls or a refugia) within the radius of dispersal determine the optimal distance of dispersal. Indeed, in our simulation, a migrating individual that met a welcoming patch stayed. Theses probabilities varied with the rainfall dynamics (annual mean, rainfalls patterns) and the number of refugia.

Being uncontrollable, we would reasonably suppose that the environment drives the persistence factors in an arid context. Our results support this. Precipitations, and the associated resources, are major components influencing the persistence probability of a population. In arid environments, if resources are not renewed by precipitation, a population will go toward local extinction.

The mean number of annual rainfalls also increased the persistence rate and determined firstly the necessity of refugia and dispersal, and secondly the extent to which they are important (hypothesis 3). Rainfall alone had a very steep relation with persistence rate. In our cases of fixed and random patterns passing from a mean of 12 to 25 rainfalls per years made persistence without refugia possible. In the cyclic

pattern, that clear threshold is absent, as population extinction remains possible even with 50 rainfalls if refugia are rare or dispersal is limited.

The pattern of rainfalls had a major effect in the sense that the cyclic *La Niña* dynamic was not easy to overcome : populations had to cope with long periods of low resources. Often, they needed abundant refugia and long distance dispersal for a chance to persist. The five arid pattern rainfall treatments (5, 12, 25, 37, 50) in arid pattern differed only in the rainfall frequency during the wet period (two years over a cycle of nine) and showed low impact on persistence rate (odds ratio; arid= 1.017, proportional =1.132, fixed/random=1.198). This suggests that it is primarily the rainfall frequency in the dry period that drives the odds of persistence. Precipitation in wet years, no matter how abundant, will not always compensate for prolonged periods with very few rainfalls. Therefore, populations are more sensitive to rainfall frequency during the drought period than during the wet period.

On the other hand, the fixed and random patterns show surprisingly very similar results, even though we thought that the variation in annual rainfalls would impact persistence rate due to the possibility for prolonged periods of few rainfalls. The dry years were not always successive, so the years with abundant rainfalls compensated adequately.

The way the simulation is programmed, the landscape is a matrix of sustainable and unsustainable patches, depending on changes in support capacity. An unsustainable patch sees its support capacity reach zero. Spatially, the unsustainable patches fragment the landscape. Fragmentation of habitat is an important driver of extinction (Fahrig, 2003). Hill and Caswell (1999) showed through patch-occupancy and

cellular-automata models that the amount of habitat loss that a population can tolerate depends on the spatial arrangement of suitable and unsuitable habitat (Hill et Caswell, 1999). They suggest that a population in a randomly fragmented landscape occupies less territory and is more susceptible to extinction in a spatially explicit model than in a patch-occupancy model. In the simulation, the rainfalls were randomly distributed in space, avoiding spatial autocorrelation. If rainfall had been spatially autocorrelated, we would have observed regions receiving more precipitation than others, and rodent populations would have aggregate more in those areas, probably enhancing the persistence probability. This underlines the importance of taking the spatial distribution of resources into account when assessing persistence. Refugia and dispersal enhance the connectivity of the landscape, which is known to enhance access to sustainable patches rich in resources (Taylor *et al.*, 1993).

Surprisingly only a few rainfalls and/or refugia appear to suffice in assuring population persistence. In our simulation, refugia were one square kilometer wide, and usually, 100 refugia were sufficient to enhance greatly the persistence probability (more for the cyclic patterns). This represent only 1 % of the whole landscape (10 000 km^2). In some cases only 10 refugia (0.1% of the landscape) suffice to promote persistence. It is similar for rainfall. 25 rainfalls per year seemed to ensure persistence, but those rainfalls covered only 2,25 % of the landscape. Rodents do not seem to need a lot of refugia or precipitation to persist minimally in that landscape.

One thing to consider though is that beside drought, other dangers, such as predation, were not explicitly incorporated in our model. Although the response is delayed, booms in predator densities usually follow heavy rainfalls and reduce rodent population densities (Letnic et Dickman, 2005). Additionally, in the Simpson desert, the spinifex vegetation dries up quickly with drought and that often leads to wildfires

in the desert. This loss in vegetation cover can exacerbate predation risk (Letnic et Dickman, 2005). While neither predation nor fire is explicitly present in our model the consequences of the factor "resource depletion" (set at 65% per year) may include loss due to fire or to predation.

Many parameters of the simulation were fixed based on field observations and/or preliminary analysis. One parameter stands out for its implication in demographic output: the depletion rate, set to 65%. At the end of each loop (year), the resources dropped to 35% of their previous year's value. Preliminary simulations showed that a lower percentage of depletion changed the results substantially. Slower depletion rates produced higher persistence rates, spatial occupation and density. Increasing the rainfall area, currently at 9 km^2 also increased persistence, occupation and density. A field analysis of depletion rates and the spatial component of rainfalls would help increase the resolution of our simulations.

2.5.1 Model extension

In our case, extinction has been declared when the population outside the refugia reached zero (refugia persistently supported some individuals). Because refugia always contain at least a few individuals this could produce a paradox in which the global population can «recover» from extinction when rains falls near a refuge. There were «resurrection» events in 50,0 % of the extinction cases. 65,8 % of the resurrected populations lasted only for a short period and remained around refugia. We easily excluded those situations from the persistence case, but that was not always the case. 7,6 % of the extinction cases happen only once and when « resurrected »,

produced persistent resurrected populations. Resurrection, as extinction, sometimes occurred repeatedly (up to 8 times) during a simulation so drawing the line between a viable and unviable population became somewhat arbitrary. Our extinction scenario is one possible view, but changing the definition could lead to different results (essentially to easier persistence). Taking resurrection into account would enhance the importance of refugia, because it was possible only via refugia. Although not included in results of the present paper, repetitive «resurrection» events could correspond to what is observed on the field — species absent for a prolonged period before erupting again. In our simulations populations remained extinct outside refuges for less than 10 years 64% of the time and less than 20 years 79% of the time. In this case, we may have underestimated the importance of refugia. However, we doubt that an alternate extinction scenario would change the overall pattern of our results.

The spatial occupancy of a population raises another series of questions leading to arbitrary decisions about what we consider a viable global population. We observed that during resource booms, species abundance and therefore spatial distribution all increased. This is supported by the trapping results of small rodents from many studies (Dickman, C. R. *et al.*, 1999 ; Letnic et Dickman, 2005 ; Pavey et Nano, 2013). According to our results, this is unlikely to show the whole portrait. Empirical data from trapping grids lack the resolution and the scale of our simulation. At most, our simulated populations did not occupy more than a third of the simulated desert. So, field researchers may over-estimate extinction cases, when they observe it on a local scale as the species is possibly present elsewhere. Our conclusions propose a high degree of heterogeneity in the spatial distribution — abundance and presence — of a population during resource booms.

2.5.2 Conclusion

The use of refugia and the mobility of species are intrinsically linked and they must be assessed together. These factors may not suffice to ensure persistence if resources are too scarce. Furthermore, refugia are important only if dispersal permits the individuals to benefit from them.

In determining the use and need of drought persistence factors in an environment, one must observe the quantity and distribution of resources over the landscape and over time. Furthermore, the regularity of resource pulses and thus pattern of rainfall cycles are very important factor in determining the probability of persistence of a population in a desert. Persistence without refugia is possible if precipitations are frequent and regular, especially if individuals can migrate at least a few kilometers. On the other hand, refugia are primordial if the precipitation pattern is cyclic and presents prolonged periods of drought.

The precipitation regime will be especially important in a period of rapid climate change. Temperature and precipitation are subject to change through global warming (Greenville *et al.*, 2012). In our model, increasing temperature could produce a higher depletion rate (higher evapotranspiration), meaning resources will dry up faster (Goyal, 2004). Our preliminary analyses showed that this parameter has a strong influence on persistence probability. Changes in the precipitation pattern in arid environment are also predicted (Aiguo, 2011). Our cyclic pattern produced generally low persistence rates. If the rainfall cycle becomes more pronounced (longer or drier periods of low rainfall) persistence of small desert rodents will become much more

difficult. In fact, persistence in the desert landscape would necessitate the use of more abundant refugia and dispersal over greater distances.

3. CONCLUSION GÉNÉRALE

Notre objectif était d'identifier le rôle des refuges et de la dispersion dans la persistance des espèces de rongeurs dans un environnement désertique. La dynamique de ces populations est semblable à celle de leurs ressources. Les précipitations sont irrégulières et génèrent des pulsations intenses, brèves et rares de ressources dans le temps et dans l'espace. Cette hétérogénéité dans l'accessibilité des ressources rend difficile la survie des rongeurs et la persistance des populations à l'échelle du paysage.

Pour approcher le problème, une échelle spatiale et temporelle étendue est de mise. Nous avons donc miser sur une simulation, sous la forme d'un automaton cellulaire couplé à des paramètres démographiques. Nous avons donc programmé une matrice dynamique représentant un désert virtuel de 10 000 km^2, et dont la population fluctue sur une période de 100 années, selon une dynamique de ressources stochastique selon une série de patrons.

Après 295 648 simulations, les résultats indiquent que l'abondance (moyenne annuelle) et la régularité (patron) des ressources ont une incidence importante sur la persistance de l'espèce et sur l'impact des refuges et de la dispersion. Il s'avère que le nombre de refuges et la distance de dispersion deviennent importants pour la persistance lorsque l'accessibilité des ressources est modérée. Ces «facteurs» sont insuffisants quand les ressources sont très rares, et superflues lorsque les ressources sont abondantes. Une longue dispersion ou un grand nombre de refuges peuvent parfois compenser pour une faible valeur de l'autre facteur. La régularité des ressources est aussi déterminante pour une population dans le désert. La dynamique cyclique de précipitations commune aux déserts — une longue période de sécheresse

et une courte période de pluie — diminuent de beaucoup les probabilités de persistance d'une population dans cet habitat, par rapport à des précipitations régulières avec faible variation inter-annuelle. L'occupation spatiale et l'abondance de nos populations simulées suivent le même patron que la persistance. Quand les précipitations et les refuges sont rares, et que les animaux migrent sur une faible distance, la densité de la population et le nombre de cellules occupées diminuent jusqu'à l'extinction.

Les fluctuations d'une population dépasse souvent les échelles permises par les études sur le terrain. La durée des études empiriques ne dépasse pas, pour l'instant, quelques années et les contraintes d'échantillonnages (capture) ne permettent pas une très grande échelle spatiale. En ce sens, notre modèle, une simulation spatialement et temporellement explicite, offre un important pouvoir de prédiction car la résolution y est grande.

Comprendre les facteurs permettant la persistance de population dans un milieu aride est une étape important dans le processus de conservation des espèces menacées. Les prédictions générées par notre simulation peuvent soutenir les efforts de conservation en soulignant l'importance de la distribution spatiale et temporelle des ressources associées à l'espèce et l'impact des refuges (et leur abondance) sur la persistance de l'espèce dans la région.

Pour répondre à notre problématique, nous avons programmé des pulsations de précipitations dans un désert. Par contre, une différente définition est aussi possible. Des simulations semblables ont été faites pour décrire des feux de forêts comme étant des pulsations (Hill et Caswell, 1999). Plusieurs ont observé la dispersion de graines pour la persistance de populations d'arbres (Green, 1989). Outre la dynamique de ressources, notre simulation s'appliquerait aussi à d'autres espèces. Les rongeurs

marsupiaux ont été un choix évident dû à la particularité des fluctuations dans leur densité et abondance. Par contre, une telle simulation pourrait aussi être pertinente pour une autre espèce de mammifères, de reptiles ou d'amphibiens terrestres. La dispersion serait différente pour des oiseaux pouvant facilement se déplacer sur de longues distances. Leur grand pouvoir de dispersion diminuerait surement le besoin en refuges.

Pour conclure, il est à noter que notre modèle est très versatile au niveau des modifications possibles. Les patrons de précipitations peuvent être modifié pour d'autres dynamiques — pluies non-aléatoire dans l'espace, pluies touchant tout le territoire, variation dans l'aire des pluies,... — dans le but de tester d'autres hypothèses, incluant des prédictions au niveau de l'impact d'un réchauffement climatique sur les populations désertiques. La variation phénotypique peut être incluse dans la simulation – ce qui permettrait d'étudier l'évolution des stratégies de dispersion par exemple. Plusieurs populations en compétition interspécifique (ou prédation) peuvent être inclus dans la simulation. Les refuges, comme les ressources, ont une valeur importante à l'intérieur d'un habitat donné et sont peut-être sujet à une compétition (par exploitation ou par interférence) entre les espèces de micro-mammifères.

ANNEXE A

SCRIPT R POUR LA SIMULATION

```
#####Preparing the export file
write.table(rbind(c("identifiant","Simulation","undrying.rate","growthrate.max","rain.nb.max","rain.ra
dius.max","pop.initiale","nb.refuges","nb.migration","rain.k","0","]0-1]","]1-10]","]10-25]","]25-50]",
"]50-100]","]100-1000]","]1000-10000]","]>10000","year","rain",
"Moy.pop","Pop.total","Capacite.total","Nb.colonise","Statut")), file="data.rain.fixe.csv",
row.names=F, col.names=F, append=T, sep=",")

#####Loop for replicates (here 2000 replicats)
for(r in 1:2000){

#####Variables
capacite.initial.desert <- 10
capacite.initial.refuges.multiplicateur <- 1000
capacitemin.refuges <- 100
undrying.rate <- 0.35
growthrate.max  <- 5
rain.nb.max <- 5
rain.radius.max <- 1
rain.k <- 1000
pop.initiale <- 2
pop.refuges.initial <- 20
nb.refuges <- 5
nb.migration <- 3
pop.min.refuges <- 20
year <- 0
simulation <- sample(1:10000000,1)
identifiant <- c("Fixe",simulation)
#sample(c(0,1,2,5,7,9,10),1)
mat.simpson.sans.refuges <- matrix(capacite.initial.desert, nrow = 100, ncol = 100)
i <- c(-1,0,1,10,25,50,100,1000,10000,10000000000)
Variables <-
rbind(c(identifiant,undrying.rate,growthrate.max,rain.nb.max,rain.radius.max,pop.initiale,nb.refuges,n
b.migration,rain.k))
zero <- rbind(c("","","",""))
quatorze <- rbind(c("","","","","","","","","","","","","","",""))
neuf <- rbind(c("","","","","","","","","",""))
rain.dataframe <- NA

#####Simulation #clearing matrices and preparing treatment variables
 nb.migration <- sample(c(1,2,3,4,5,8),1)
 rain.nb.max <- sample(c(5,12,25,37,50),1)
 nb.refuges <- sample(c(1,10,50,100,200,350),1)
 simulation <- simulation+1
 identifiant <- c("Fixe",simulation)
```

```
 Variables <-
rbind(c(identifiant,undrying.rate,growthrate.max,rain.nb.max,rain.radius.max,pop.initiale,nb.refuges,n
b.migration,rain.k))
 write.table(rbind(c(Variables,quatorze,"DEBUT")), file="data.rain.fixe.csv", row.names=F,
col.names=F, append=T, sep=",")
 mat.N <- matrix(pop.initiale, nrow = 100, ncol = 100)

##### Random instalation of the refuges
 mat.refuges <- matrix(1, nrow = 100, ncol = 100)
 for(o in 1:nb.refuges) {
  y <- round(runif(1, 1, 100))
  x <- round(runif(1, 1, 100))
  mat.refuges[x,y] <- capacite.initial.refuges.multiplicateur}
 mat.N[which(mat.refuges==capacite.initial.refuges.multiplicateur)] <- pop.refuges.initial

##### initial K of desert cell
  mat.simpson.K <- mat.simpson.sans.refuges*mat.refuges

#####  Start of the loop (100 years)
  for(r in 1:100) {

##### Rain
   year <- year+1
   mat.pluies <- matrix(0, nrow = 100, ncol = 100)
   rain <- rain.nb.max
   for(r in 1:rain){
    y <- round(runif(1, 3, 97))
    x <- round(runif(1, 3, 97))
    mat.pluies[(x-rain.radius.max):(x+rain.radius.max),(y-rain.radius.max):(y+rain.radius.max)] <-
rain.k;}
   mat.simpson.K <- mat.simpson.K+mat.pluies;

##### Growth
   mat.N <- mat.N+(mat.N*growthrate.max*(1-(mat.N/mat.simpson.K)))
   #mat.N <- mat.N+(mat.N*growthrate.max)

##### Local extension
   mat.N[which(mat.N<1*runif(1))] <- 0

##### Migration
   for(m in 1:nb.migration){
    mat.emigre <- mat.N-mat.simpson.K
    mat.emigre[which(mat.emigre<0)] <- 0
    mat.N <- mat.N-mat.emigre
    pourcent <- mat.N*0.1
    pourcent[which(mat.refuges==capacite.initial.refuges.multiplicateur)] <-
ifelse(mat.N[which(mat.refuges==capacite.initial.refuges.multiplicateur)]<pop.min.refuges, 0,
pourcent[which(mat.refuges==capacite.initial.refuges.multiplicateur)])
    mat.emigre <- (mat.emigre+pourcent)/4
    mat.N <- mat.N-pourcent
    mat.emigre <- rbind(mat.emigre[100,],mat.emigre,mat.emigre[1,])
    mat.emigre <- cbind(mat.emigre[,100],mat.emigre,mat.emigre[,1])
    mat.imigre <- matrix(NA, nrow = 100, ncol = 100)
```

```
    for(y in 1:100)
    {for (x in 1:100){
      mat.imigre[x,y] <- sum(mat.emigre[(x+1),(y+1+1)],mat.emigre[(x+1+1),(y+1)],mat.emigre[(x
+1),(y+1-1)],mat.emigre[(x+1-1),(y+1)])}}
    mat.N <- mat.N+mat.imigre}

##### Elimination over K
  mat.mort <- mat.N-mat.simpson.K
  mat.mort[which(mat.mort<0)] <- 0
  mat.N <- mat.N-mat.mort

##### Ressource depletion
  mat.simpson.K <- mat.simpson.K*undrying.rate
  mat.simpson.K[which(mat.refuges==capacite.initial.refuges.multiplicateur)] <-
ifelse(mat.simpson.K[which(mat.refuges==capacite.initial.refuges.multiplicateur)]<capacitemin.refuge
s, capacitemin.refuges, mat.simpson.K[which(mat.refuges==capacite.initial.refuges.multiplicateur)])

  Moy.pop.total <- mean(mat.N)
  freq.N.sans <- rbind(table(cut(mat.N[which(mat.refuges<capacite.initial.refuges.multiplicateur)],
i)))
  data.N.sans <- as.data.frame(freq.N.sans)
  Nb.colonise <-
length(mat.N[which(mat.N[which(mat.refuges<capacite.initial.refuges.multiplicateur)]>1)])
  Capacite.total <- sum(mat.simpson.K[which(mat.refuges<capacite.initial.refuges.multiplicateur)])
  mat.N.sans <- mat.N
  mat.N.sans[which(mat.refuges==capacite.initial.refuges.multiplicateur)] <- 0
  mat.N.sans[which(mat.N.sans<1)] <- 0
  Pop.total <- sum(mat.N.sans)
  if(Nb.colonise>2000)
{write.table(rbind(c(Variables,data.N.sans,year,rain,Moy.pop.total,Pop.total,Capacite.total,Nb.colonise
,"pic")), file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}
  if(Nb.colonise>0 & Nb.colonise<2000)
{write.table(rbind(c(Variables,data.N.sans,year,rain,Moy.pop.total,Pop.total,Capacite.total,Nb.colonise
,"faible")), file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}
  if(Nb.colonise<1)
{write.table(rbind(c(Variables,data.N.sans,year,rain,Moy.pop.total,Pop.total,Capacite.total,Nb.colonise
,"mort")), file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}}

##### Data
 if(Nb.colonise<1){write.table(rbind(c(Variables,quatorze,"EXTINCTION")),
file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}
 if(Nb.colonise>0 & Nb.colonise<2000) {write.table(rbind(c(Variables,quatorze,"SURVIE")),
file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}
 if(Nb.colonise>2000) {write.table(rbind(c(Variables,quatorze,"COLONISATION")),
file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}
 if(Moy.pop.total==0){write.table(rbind(c(Variables,quatorze,"ANNIHILATION")),
file="data.rain.fixe.csv", row.names=F, col.names=F, append=T, sep=",")}}
```

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